Swimming energetics of the Barents Sea capelin (*Mallotus villosus*) during the spawning migration period

Jane W. Behrens [a,*], Kim Præbel [b], John F. Steffensen [a]

[a] *Marine Biological Laboratory, University of Copenhagen, Strandpromenaden 5, DK-3000 Helsingør, Denmark*
[b] *Norwegian College of Fisheries Science, University of Tromsø, 9037 Tromsø, Norway*

Abstract

The Barents Sea capelin, a schooling species, undertakes extensive migrations against the predominating current north of Norway to its spawning grounds along the Norwegian and Russian coasts. Low swimming costs (i.e. high efficiency) at cruising speeds would be advantageous for capelin, enabling allocation of more energy to reproduction. A high oxygen uptake capacity may however also be beneficial, considering the difficulty of strenuous swimming against the predominant current, and to avoid predators. To investigate the swimming energetics of the Barents Sea capelin, the relationship between rate of oxygen uptake, MO_2 (mg O_2 kg^{-1} h^{-1}), and swimming speed was investigated at 5 °C. A power and an exponential function described the correlation between MO_2 and swimming speed almost equally well as determined by the correlation coefficient. The power function described the relationship as $MO_2 = 101.624 + 43.5U^{2.042}$, where U was the swimming speed in body lengths per second (bl s^{-1}) and 101.6 an estimate of the standard metabolic rate (SMR, mg O_2 kg^{-1} h^{-1}). The exponential function gave $MO_2 = 85.747e^{0.591U}$ with U being the swimming speed (bl s^{-1}) and 85.7 an estimate of the SMR (mg O_2 kg^{-1} h^{-1}). The active metabolic rate (AMR, mg O_2 kg^{-1} h^{-1}), the oxygen uptake measured at the critical swimming speed (U_{crit}), was 532 mg O_2 kg^{-1} h^{-1}, hence resulting in a scope for activity (SFA) of 5.2 or 6.2, depending on the model for SMR estimation. The capelin was able to sustain U_{crit} of 3 bl s^{-1}, or ~51 cm s^{-1}. The relationship between cost of transport (COT) and swimming speed was characteristically U-shaped, with minimum cost of transport (COT$_{min}$) between 218 and 225 mg O_2 kg^{-1} km^{-1}, at an optimal swimming speed (U_{opt}) within the range of 1.5 to 1.7 bl s^{-1}. The swimming energetics of capelin was related to its migratory behaviour and the results compared to other pelagic species. Finally, the limitations involved with working with a schooling species were discussed, in addition to how choice of model for description of costs associated with swimming generally may influence parameter estimation.
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1. Introduction

Barents Sea capelin, *Mallotus villosus villosus* (Müller, 1776), is a pelagic, schooling species, belonging to the family Osmeridae. It inhabits the arctic and sub-arctic waters, where it is a key prey item for several fish species (e.g. Atlantic cod, *Gadus morhua*), and marine mammals (e.g. harp seal, *Pagophilus groenlandicus*) (Nilssen et al., 2000). In early spring, the sexually mature fish (2–4 years old) leave the offshore waters of the Barents Sea where they spend most of their lives and migrate south against the predominating

* Corresponding author. Tel.: +45 3532 1972; fax: +45 49261165.
E-mail address: jwbehrens@bi.ku.dk (J.W. Behrens).

current north of Norway. This is a substantial and energetically demanding migration, taking the fish to their spawning grounds along the Norwegian and Russian coasts (Ozhigin and Luka, 1985; Gjøsæter and Loeng, 1987). The metabolic rate of fish includes many different energy-demanding processes, which can be separated into the standard metabolic rate (SMR), the active metabolic rate (AMR) and the elevated metabolism caused by the joint processes involved with feeding, termed the specific dynamic action (SDA). SMR is the minimum maintenance oxygen consumption of a resting, post-absorptive fish, whereas AMR is the metabolic rate of a fish during maximum sustained swimming. The swimming speed where the metabolic cost per unit distance is minimised (i.e. U_{opt}, Videler, 1993) has been suggested as the speed associated with long-distance migration of saithe and sockeye salmon, though presumably only in environments with slow currents (less than 0.25 m s^{-1}) for salmon (Madison et al., 1972; Quinn, 1988; Hinch and Rand, 2000; Steinhausen et al., 2005). There is however a great deal of uncertainty regarding which speeds fish primarily uses in the wild and for what purposes. Nonetheless, it would be energetically beneficial for capelin to swim at U_{opt} while migrating. It may however also be an advantage to get to the spawning grounds first, e.g. if there is competition for spawning grounds or females, that is why swimming faster than U_{opt} and closer to the critical swimming speed, U_{crit}, could increase the chances of reproducing. In the laboratory, measurements of swimming performance are commonly done by determining U_{crit}, as defined by Brett (1964), where AMR is measured as the rate of oxygen uptake at U_{crit}. The ratio between AMR and SMR, defined as the scope for activity (SFA) by Fry (1957), is the energetic frame for aerobic metabolism and often used to reflect swimming performance. For capelin a substantial SFA may help surmount the difficulties of swimming against the current and escape predators. The cost of transport (COT), the amount of oxygen required per unit distance per unit weight, is at a minimum (COT$_{min}$) at U_{opt}, and these parameters give a fair base for comparison between species of total costs associated with and time taken to cover a particular distance if swimming at U_{opt}.

Only sparse information is available of oxygen uptake during swimming of schooling pelagic species, and to the authors' knowledge there have been no previous reports on swimming energetics of capelin. Consequently, we aimed to examine the relationship between swimming speed and oxygen uptake for capelin in a flume-type swimming respirometer. The experimental fish were caught while undertaking their extensive spawning migration; this is why we discuss the results in the light of that, and also how it compares to other species. Finally, we attempt to evaluate the experimental limitations due to working with a schooling species, and how choice of model to describe the costs of swimming generally will affect estimations of the descriptive parameters.

2. Materials and methods

2.1. Fish

Sexually mature male and female Barents Sea capelin were caught in the middle of March 2004 in the Barents Sea, north of Hjelmsøy (71.2°N, 24.4°E), from R/V Jan Mayen using a pelagic trawl. The fish were transported to Tromsø (70°N), and held at the Norwegian College of Fisheries Science in square indoor flow-through tanks (100 × 100 × 50 cm with approximately 350 l of water) at 5 ± 0.2 °C, 34‰, and natural photoperiod of Tromsø. The fish were not fed for a minimum of 48 h before experimentation. Approximately one week after capture both male and female capelin began to spawn.

2.2. Swimming respirometry

Only mature males (weight 19.6–33.6 g, length 16.5–18.5 cm) in good condition were used for the experiments, as significant difference in SMR between genders has been noted previously (Karamushko and Christiansen, 2002). For measurements of oxygen uptake in relation to swimming speed, 7 groups of three fish were swum together. A group of three was chosen as a compromise between the need for high sensitivity of oxygen uptake measurements (i.e. a high enough mass of fish relative to respirometer volume) and that the fish swam in a more regular manner when in a small group, presumably due to their schooling behaviour. However, the number of fish swum together in the respirometer was limited by the space available for the fish to move without interfering with each other.

The swimming respirometer was a computerized automated, intermittent flow-through respirometer (Steffensen et al., 1984) with a volume of 8.3 l and a swimming section of 7 × 9 × 30 cm. It was submerged in a larger 30 l (20 × 23 × 66 cm) tank, held at a stable temperature of 5 ± 0.2 °C. Water flow in the swimming section was generated by a voltage-controlled motor and propeller, where the voltage was calibrated against